

OBSERVATIONS ON TWO SPECIES OF HYPERIID AMPHIPODS ASSOCIATED WITH THE CTENOPHORE *PLEUROBRACHIA BACHEI*

MARILYN FLORES¹ AND GARY J. BRUSCA²

ABSTRACT: Two species of hyperiid amphipods (*Hyperoche medusarum* and *H. mediterranea*) were found in symbiotic associations with the ctenophore *Pleurobrachia bachei*. *H. mediterranea* has not previously been reported from this ctenophore. Adult amphipods were most frequently encountered on the exterior of the host, or forming excavations in the surface. Immatures were most abundant within the mesoglea of the ctenophore. Behavioral observations on living specimens are discussed and related to the method of entrance into the host by the amphipods.

Symbiotic relationships between pelagic hyperiid amphipods and various host organisms (medusae, ctenophores, salps) have been noted by several authors (Bowman, Meyers, and Hicks, 1963; Brusca, 1967, 1971; Hardy, 1965; Laval, 1963, 1966, 1968; Schellenberg, 1942; Stephensen, 1923; Steuer, 1911), but few of these reports discuss the nature of the associations. In at least one instance, (*Hyperia galba* on the scyphomedusa *Cyanea capillata*), post mortem gut analyses of the amphipod revealed nematocyst capsules and the relationship was reported as parasitic (Dahl, 1959). Bowman *et al.*, (1963) reported on observations of living specimens of *H. galba* on a live *C. capillata*, but actual feeding by the hyperiid was not seen, and Dahl's conclusions remain unsupported by direct evidence. Most of the related literature consists of reports of occurrence of members of the family Hyperiididae.

We intend to elaborate on the association between *Hyperoche medusarum* and the ctenophore *Pleurobrachia bachei*, previously reported by Brusca (1971), and to present observations on the association between *H. mediterranea* and *P. bachei*. We have found no mention of the latter relationship in the literature. All of the specimens discussed here were collected from northern California waters either with plankton nets aboard the RV/CATALYST within a few miles of the entrance to Humboldt Bay, or by finding freshly stranded ctenophores on the mud and sand flats of the bay itself. Collections were made during the months of June and July, 1972.

SYSTEMATICS OF *H. MEDUSARUM* AND *H. MEDITERRANEA*

The genus *Hyperoche* is distinguished from other members of the family Hyperiididae by having

gnathopods one and two chelate, with the carpal prolongation of the second pair compressed and blade-like. In the two species discussed here, the carpal process of the first gnathopods are similar in shape.

Only about 45 specimens collected during this study were large enough to identify with certainty. The remaining individuals were unpigmented juveniles (less than 1 mm in length) and immatures (1–3 mm in length), and could not be identified or sexed. The epimeral plates of these young amphipods were observed under 430× magnification, but could not be assigned to either species as described below.

The separation of *H. medusarum* from *H. mediterranea* is based upon the shape of the epimeral plates of pleonites 1–3. Hurley (1955) described these two species from specimens taken in New Zealand waters. Figures 1 and 2 picture the epimeral plates and gnathopods from males and females, and illustrate the specific traits as observed in the animals collected during the present study.

Pleonites 1–3 possess postero-ventral points in *H. medusarum* (Fig. 1 A, D), whereas, these plates are generally rounded and blunt in *H. mediterranea* (Fig. 2 A, D). Some variation was noted when examining individuals for this characteristic, and the specimens figured are individuals which show the described shapes. Some of the amphipods displayed less prominent, but distinct points, and in one instance a point was seen on the second plate; none was present on either the first or the third plate. The extent to

¹ P.O. Box 505, Lower Lake, California 95457.

² Ministry of Fisheries, c/o U.S. Peace Corps, P.O. Box 379, 44 R. Seenevassen St., Port Louis, Mauritius, Indian Ocean.

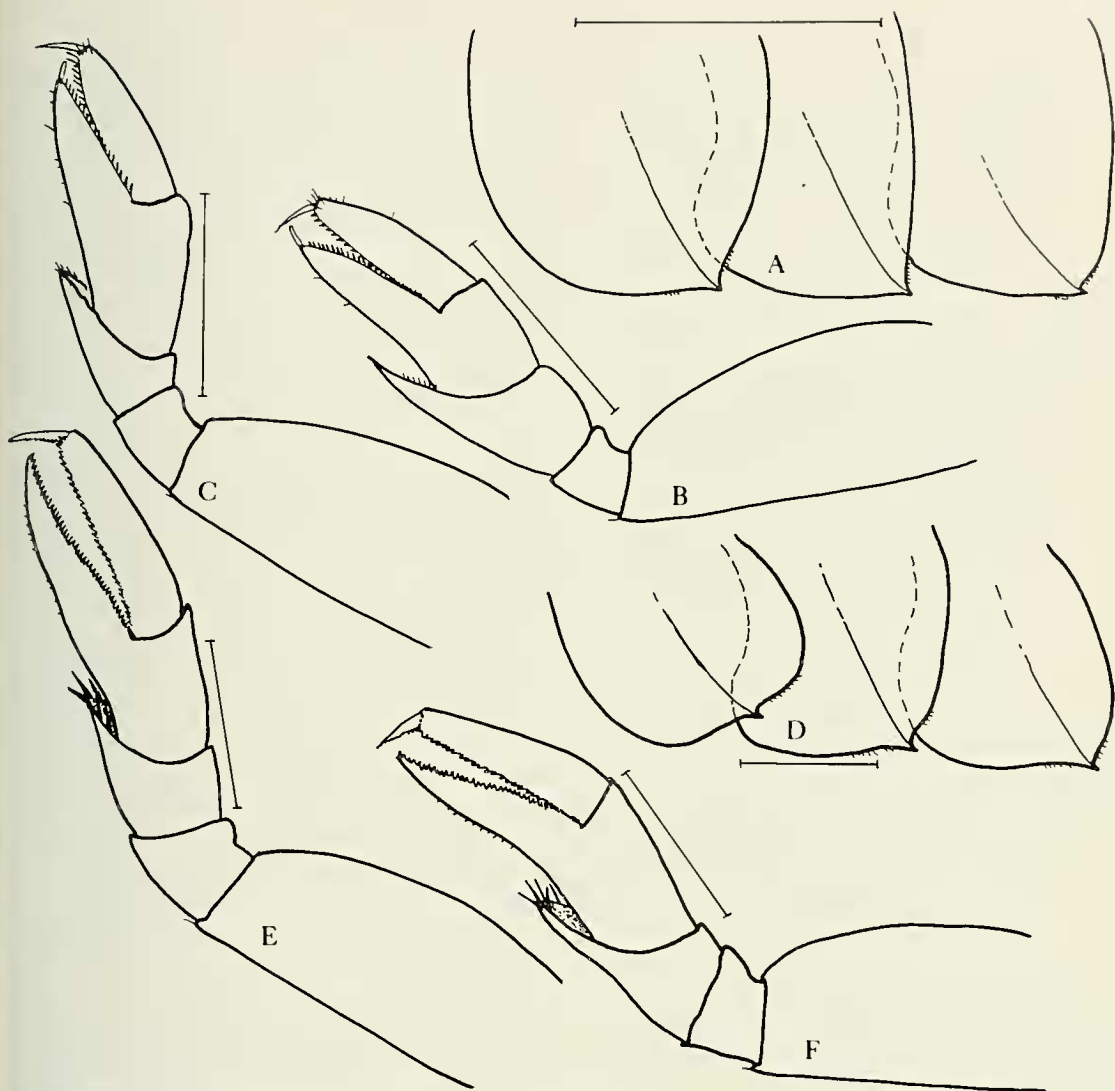


Figure 1. *Hyperoche medusarum*. A (♀), epimera of pleonites 1, 2, 3; B (♀), gnathopod 1; C (♀), gnathopod 2; D (♂), epimera of pleonites 1, 2, 3; E (♂), gnathopod 2; F (♂), gnathopod 1. Total length of ♀ = 4 mm, total length of ♂ = 6.5 mm. All scale lines = 0.5 mm.

which these intermediate forms are present in the natural population is unknown, but it should be of interest to examine a larger series for possible taxonomic implications.

The gnathopods of both species are similar, with the following differences. The meeting edges of the chelae appear quite heavily toothed in *H. medusarum* (Fig. 1 B, C, E, F) when compared with the fine setation of the respective claw margins on *H. mediterranea* (Fig. 2 B, C, E, F). In addition, the extension of the merus along the posterior edge of the carpus bears 5–7 large distal

spines in *H. medusarum* (males), which are absent from *H. mediterranea*. Hurley (1955) reported these spines in female *H. medusarum* as well, but the specimens studied here showed only a fine to moderate setation.

Although *H. medusarum* has been reported from the northeastern Pacific, *H. mediterranea* was previously known only from the Mediterranean Sea, and the south Pacific near New Zealand. It is likely that these species will be shown to have wider distributions as more samples become available from around the world.

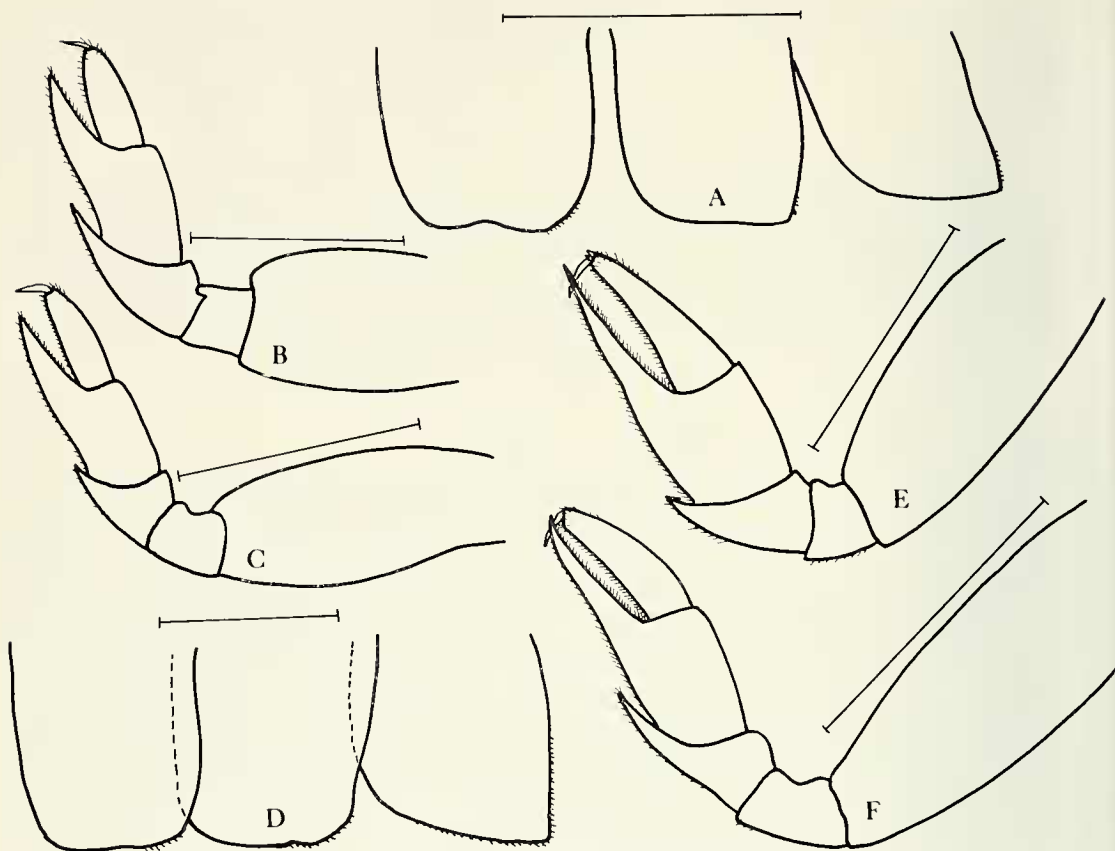


Figure 2. *Hyperoche mediterranea*. A (♀), epimera of pleonites 1, 2, 3; B (♀), gnathopod 1; C (♀), gnathopod 2; D (♂), epimera of pleonites 1, 2, 3; E (♂), gnathopod 2; F (♂), gnathopod 1. Total length of ♀ = 3 mm, total length of ♂ = 5.5 mm. All scale lines = 0.5 mm.

MATERIAL EXAMINED AND LOCATION WITHIN THE HOST

Detailed counts were made of the amphipods associated with 50 preserved *Pleurobrachia bachei*. Every ctenophore housed at least one hyperiid, and one individual contained five. Thirty-two amphipods had dropped from the hosts during preservation (17 adults and 15 young) and 107 were removed from inside the ctenophores (106 young and 1 adult). The examination of the 50 specimens thus yielded a total of 139 hyperiids. This is a marked increase in density over the 1971 report by Brusca of 24 hyperiids in 135 *P. bachei*. Unfortunately, earlier work analyzed undated samples, so any seasonal significance to the difference remains unclear.

The specific locations of the amphipods removed from the preserved ctenophores were as follows: Adults (total = 18)—*H. medusarum*,

(6 specimens; dropped from surface); *H. mediterranea*, (12 specimens; 11 dropped from surface, 1 in mesoglea). Unidentifiable young (total = 121)—15 specimens, dropped from surface; 101 specimens, in mesoglea; 2 specimens, imbedded in surface; 2 specimens, partially imbedded in gut wall (aboral canal); 1 specimen, inside pharynx.

In addition to the above data on preserved individuals, several living adult amphipods were observed on freshly collected ctenophores. Counts were not made during these behavioral studies.

OBSERVATIONS ON LIVING SPECIMENS

About 20 living ctenophores were examined in a search for active hyperiids. Most of the amphipods noted were immature and imbedded in the mesoglea; these remained stationary while slowly

moving their pereopods and gnathopods. While some of these young hyperiids moved the gnathopods around the area of their mouthparts, definite feeding activity could not be confirmed.

In two instances live, unpigmented juveniles (less than 1 mm long) were seen moving about within the gut canals of the host. Although small crustaceans frequently are eaten by *P. bachei*, neither of these amphipods seemed to be affected by the digestive action of the gut. In the above two cases there was no visible damage to the gut wall. Evidence presented earlier mentioning two preserved amphipods partially imbedded in the canal walls, indicates that these young hyperiids may actually burrow into the lumen of the gut from the surrounding mesoglea. This combination of data suggests that the ctenophores must heal rapidly enough to prevent serious interference with feeding and digestion.

Brusca (1971) reported that the three adult *H. medusarum* he found in *P. bachei* were imbedded in the mesoglea. Two of these specimens were completely encased and the hosts showed no evidence of external damage. The third had contact with the exterior through a hole in the surface of the ctenophore. This opening was oval and about the size of the amphipod's head, quite unlike the excavations observed during the present study. As is suggested for the gut wall, the body surface must also heal without permanent damage to the host.

We independently made observations on the behavior of live hyperiids located on or in the surface of the ctenophores. Upon comparing records of these separate observations, it was found that some actions of the amphipods followed consistent patterns. Two common situations were encountered and described for males and females of both species of *Hyperoche*. Some of the females were carrying ova or young in their brood pouches. Many of the amphipods crawled slowly over the surface of the host, using the posterior three pairs of pereopods. These individuals paused frequently, picking at the ctenophore with their gnathopods. It appeared that these appendages transferred material to the area of the mouthparts, but feeding could not be confirmed.

A second, more complex condition was noted in which amphipods were excavating the surface of the ctenophores. Figure 3 diagrammatically represents two specimens observed during such activities. Amphipods were seen digging in virtually all parts of their hosts, with the exception of the area immediately surrounding the mouth. In

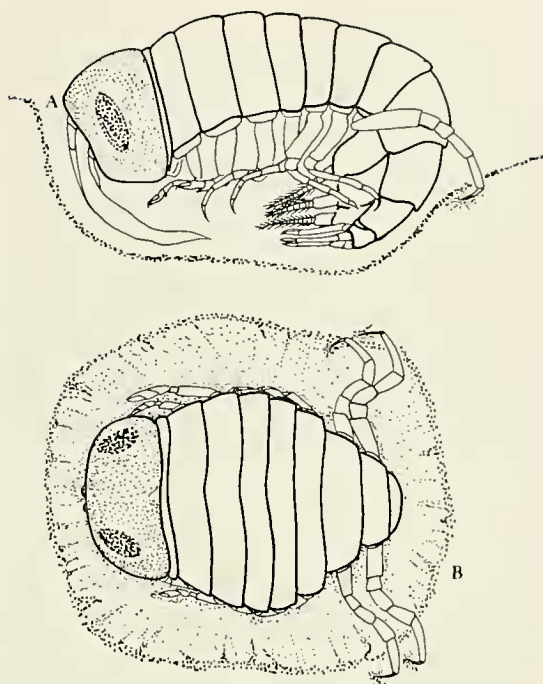


Figure 3. A, diagrammatic lateral view of 5.5 mm ♂ *H. medusarum* forming an excavation in the surface of *P. bachei*. This individual was attached only by the last pair of pereopods. B, diagrammatic dorsal view of 3 mm ♀ *H. medusarum* positioned over an excavation site. This amphipod was attached by pereopods 4 and 5.

several instances, excavation broke through comb rows, or was near tentacular sheaths. In one case, tentacles of the ctenophore were wrapped around the amphipod for several minutes with no apparent effect or evidence of colloblast release.

The hyperiids fixed themselves in position by imbedding the dactyli of any combination of the last three pairs of pereopods into the epidermis of the host. The abdomen was flexed ventrally and forward. The head and front portion of the thorax were, at this point, suspended above the excavation site. After positioning, the most common sequence of events was as follows: The head was lowered and the gnathopods picked for a few seconds at the exposed mesoglea in the depression. Some indications of passing material to the mouth were noted. Following these movements, the head was raised and the gnathopods were extended laterally. Holding this position, the pleopods were vigorously fanned for two or three seconds during which time small bits of detritus were carried out under the head in the resultant

current. Then the head was lowered and the sequence repeated.

Several less consistent behavioral patterns were noted by both observers. Occasionally the tail fan was moved in a posterior to anterior scooping motion, followed by the typical "picking and digging" activity. Other instances included pushing the sides of the excavation outward by a lateral extension of the gnathopods as the pleopods were fanned. Nearly every hyperiid which was observed for a few minutes engaged in what appeared to be a cleaning activity. The first pair of gnathopods were placed over the dorsum of the body at about the junction of the head and thorax, then brought forward over the surfaces of the cephalon and the antennae.

CONCLUSIONS

At least during the summer months, the incidence of amphipods in *P. bachei* is high (100 percent in the material examined). Most of the adult *Hyperoche* were found on the exterior of their hosts and exhibited excavating behavior, as described above. This activity may represent an invasionary process by which the amphipods enter the mesoglea of the ctenophores. This suggestion is supported by the fact that the adults are sometimes found completely imbedded within the host with no communication to the outside.

The high frequency of juveniles within the bodies of the ctenophores may be the result of releasing young either on the surface of the host or within the mesoglea after burrowing. Some mature females in this study carried ova or young, and Brusca (1971) located one female with eggs within the mesoglea. The two juveniles which were found imbedded in the surface of ctenophores could have been entering or leaving the hosts. Perhaps the relationship provides a protective nursery environment for the young amphipods. The two live hyperiids located within the gut canals of the ctenophores either entered through the mouth or burrowed through the wall from the mesoglea. The latter is suspected to be the case since those which were partially imbedded in the canal walls were in a "digging" position, with the heads deeper into the gut than the posterior portion of the body.

There does not appear to be any difference between the activities of *H. medusarum* and *H. mediterranea* in their association with *P. bachei*, and neither seems to cause permanent damage to the host.

ACKNOWLEDGMENTS

We thank the participants of the 1972 National Science Foundation Summer Institute for High School Students No. NSF GW7545 (John E. Butler, California State University, Humboldt, Director) for their help in collecting materials for this study. Special appreciation is extended to Donald Martin, California State University, Humboldt, for his enthusiasm and assistance during the Institute, and for reading the manuscript.

LITERATURE CITED

- Bowman, T., C. Meyers, and S. Hicks. 1963. Notes on associations between hyperiid amphipods and medusae in Chesapeake and Narragansett Bays and the Niantic River. *Chesapeake Sci.*, 4:3: 141-146.
- Brusca, G. J. 1967. The ecology of pelagic amphipods I: species accounts, vertical zonation and migration of Amphipoda from the waters off southern California. *Pac. Sci.*, 21:3:389.
- . 1971. Notes on the association between *Hyperoche medusarum* (Muller) (Amphipoda, Hyperiidea) and the ctenophore, *Pleurobrachia bachei* A. Agassiz. *Bull. So. California Acad. Sci.*, 69:3-4:179-181.
- Dahl, E. 1959. The amphipod *Hyperia galba*, an ecto-parasite on the jelly-fish, *Cyanea capillata*. *Nature*, 183:4577:1749.
- Hardy, A. 1965. *The Open Sea: Its Natural History*, Part I: The World of Plankton. The Riverside Press, Cambridge, Second Edition, pp. 128, 169-170.
- Hurley, D. E. 1955. Pelagic Amphipods of the Sub-Order Hyperiidea in New Zealand Waters. *Trans. Roy. Soc. New Zealand*, 83:1:119-194.
- Laval, P. 1963. Sur la biologie et les larves de *Vibilia armata* Bov. et de *V. propinqua* Stebb. Amphipodes Hypérides. *Acad. Sci. Paris*, 257: 12:1-4.
- . 1966. *Bougisia ornata*, genre et espece nouveaux de la famille des Hyperiidae (Amphipoda, Hyperiidea). *Crustaceana*, 10:2:217-218.
- . 1968. Observations sur la biologie de *Phronima curvipes* Voss. (Amphipode Hypéride) et description du male adulte. *Cahiers de Biologie Marine*, 9:348.

Schellenberg, A. 1942. Die Tierwelt Deutschlands und der angrenzenden Meeresteile nach ihren Merkmalen und nach ihrer Lebensweise. Begr. v. Friedrich Dahl. Weitergef. v. Maria Dahl u. Hans Bischoff. Gustav Fischer, Jena, 40. Tl. IV. 252 S. u. 204 Abb. Rm. 30.

(Amphipoda I). Direction of the Zoological Museum of the University of Copenhagen, p. 15.

Steuer, A. 1911. Adriatische Planktonamphipoden. Sitzungsberichte der Akademie der Wissenschaften in Wien, 130:1:672.

Stephensen, K. 1923. The Danish Ingolf Expedition, Vol. II, Part 8, Crustacea Malacostraca V.

Accepted for publication January 2, 1973.

HANNEMANIA (ACARINA: TROMBICULIDAE) AND THEIR ANURAN HOSTS AT FORTYNINE PALMS OASIS, JOSHUA TREE NATIONAL MONUMENT, CALIFORNIA

W. CALVIN WELBOURN, JR., AND RICHARD B. LOOMIS¹

ABSTRACT: The larval stage of *Hannemania hylae* (Ewing) embeds in the California Tree Frog *Hyla cadaverina* Cope and *Hannemania bufonis* Loomis and Welbourn parasitizes the Red-Spotted Toad, *Bufo punctatus* Baird and Girard at Fortynine Palms Oasis, San Bernardino County, Joshua Tree National Monument, California. Studies from May 1969 to April 1971 revealed estimated average populations of 288 frogs and 300 toads around three small ponds.

Approximately 98.9 percent of the frogs had a mean of 21.4 *H. hylae* per frog and the estimated larval populations varied from 4250 in the spring to 8500 larvae in July to September. One life cycle is completed each year, but unengorged larvae were found on frogs throughout the summer. Nearly 41 percent of the toads possessed a mean of 8 *H. bufonis* and the estimated low was 840 larvae in May to July and the high was 1350 larvae in September. Only one life cycle per year was determined, and unengorged larvae were observed only in the late summer months.

A conspicuous parasite of amphibians is the larval trombiculid mite commonly called a chigger. Larvae of four genera have adapted to amphibian hosts by embedding in the skin. Two genera, *Vercammenia* (Audy and Nadchatram, 1958) and *Anouracarus* (Vercammen-Grandjean, 1973) are known from the Asiatic-Pacific Region, whereas a third, *Endotrombicula* (Ewing, 1925), is found on amphibians in South Africa. The fourth genus, *Hannemania* Oudemans, is certainly the best developed of the intradermal chiggers, and has been found only in the New World.

The length of time as a parasite seems long for *Hannemania* larvae when compared to most other trombiculid mites. Hyland (1961) observed that in the laboratory *Hannemania hegneri* Hyland remained for at least six months on frogs of the genus *Rana*. Ewing (1926) stated that *H. hylae* was trapped in the skin, and Loomis (1956) believed that *H. eltoni* Sambon overwintered in the skin of the hosts.

The following study involves the populations and natural cycles of *Hannemania hylae* (Ewing) found on the California Tree Frog, *Hyla cadaverina* Cope, and *Hannemania bufonis* Loomis and Welbourn taken only from the Red-Spotted Toad, *Bufo punctatus* Baird and Girard at Fortynine Palms in Joshua Tree National Monument, San Bernardino County, California. This locality was selected because both the hosts and their respective chiggers were found in the same small protected area. The oasis is about 610 meters in elevation and consists of nine major ponds. This study centered around the upper three ponds.

The trees at the oasis consisted largely of California Fan Palms (*Washingtonia filifera*), Cottonwoods (*Populus fremontii*), Willow (*Salix*), and Mesquites (*Prosopis*) (Miller and Stebbins,

¹Dept. Biology, California State University, Long Beach, California 90840.